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Photosynthetic Responses of Eelgrass (*Zostera marina* L) to Light and Sediment Sulfide in a Shallow Barrier Island Lagoon

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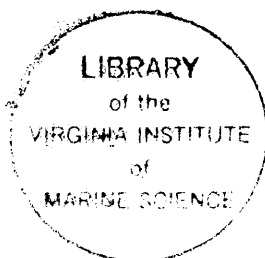
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PHOTOSYNTHETIC RESPONSES OF EELGRASS
(*Zostera marina* L.) TO LIGHT AND SEDIMENT SULFIDE IN A
SHALLOW BARRIER ISLAND LAGOON

A Thesis
Presented to
The Faculty of the School of Marine Science
The College of William and Mary in Virginia

In Partial Fulfillment
Of the Requirements for the Degree of
Masters of Art

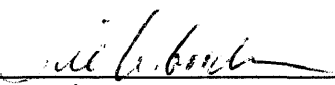
By
Jill L. Goodman
1992




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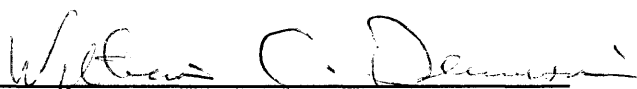
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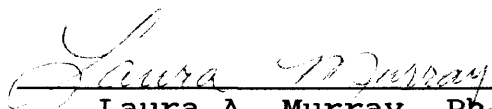
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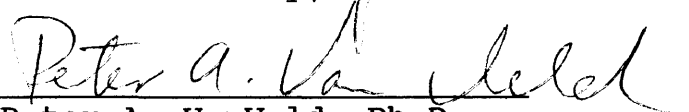

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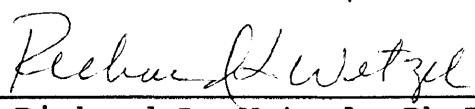

Richard L. Wetzel, Ph.D.

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This work is dedicated to my mother who, throughout my life, has encouraged and inspired me to succeed in whatever I do.

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ABSTRACT

Highly reducing sediments are prevalent where seagrasses exist. Under such anoxic sediment conditions, hydrogen sulfide accumulates as an end product of anaerobic respiration. Hydrogen sulfide can be toxic to marine macrophytes and in combination with other factors may result in severe stress and eventual loss of seagrass populations. The photosynthetic response of *Zostera marina* L. (eelgrass) to manipulations in sediment sulfide concentration and light regimes were examined in Chincoteague Bay in June of 1991. In both field and microcosm experiments screens were used to decrease downwelling irradiance by 80% and sediment sulfide levels were enriched using NaS_2 in a replicated factorial design. Photosynthesis vs. irradiance relations and leaf chlorophyll content were determined at the end of three weeks. There was no photosynthetic response of the eelgrass to decreases in light over a 21 day period. This may be due to the ability of the eelgrass in Chincoteague Bay to adapt daily to variable light. It seems there were adequate hours of light, even in the low light treatments to allow these plants to photosynthesize at normal levels. The P-max was reduced in eelgrass leaf tissue exposed to treatments of sediment sulfide above 500uM. The respiratory demand of the eelgrass is increased with sediment sulfide levels above 500uM. This implies that the maintenance cost (ie. respiratory demand) is increased as more O_2 is transported from shoots to the root rhizosphere. Total chlorophyll is also increased with sulfide concentrations above 500uM. This increase along with the decrease seen in the initial slope, implies a decrease in efficiency of light harvesting as sediment sulfide is increased.

INTRODUCTION

Seagrasses are a group of approximately 50 species (12 genera) of angiosperms growing completely submersed in saline environments (den Hartog 1970). These macrophytes flourish in embayments and other sheltered coastal areas of polar, temperate, and tropical regions of the world (Mukai et al. 1979). Despite environmental conditions which include marked fluctuations in light availability, temperature, and salinity, seagrasses are among the most productive systems in the world (McRoy & McMillan 1977, Zieman & Wetzel 1980). On a per area basis, seagrasses are more productive than cultivated corn or hay (Thayer et al. 1975). Besides providing a major source of primary production, seagrasses serve many other functions in marine systems. They are an important component in bottom stabilization and retarding of currents (Boudouresque & de Grissae 1983, Ward et al. 1984, Fonseca et al. 1982). They provide nursery grounds for fish and invertebrates and a substrate for epiphytes (Kikuchi & Peres 1977, Bulthuis & Woelkerling 1983, Borum 1985). Seagrasses are also the primary producers of detrital based food chains (Wood et al. 1969).

Zostera marina L. (eelgrass) is a temperate seagrass that grows in highly reducing sandy and muddy sediments of

coastal bays and estuaries in the Northern Hemisphere (Smith et al. 1988, Thayer et al. 1975). Eelgrass can tolerate a broad range of salinities from 10-40 ppt, and water temperatures from 0-40°C (Thayer et al. 1975). However, optimum growth and reproduction of *Z.marina* is exhibited at salinities of 10-20 ppt and temperatures between 10-20°C (Biebl & McRoy 1971).

Photosynthesis begins with the absorption of light by light harvesting chlorophyll a and b protein complexes (Salisbury & Ross 1985). Light varies from one habitat to another and may also show seasonal variation within a habitat. Adaptation of marine autotrophs to light has been demonstrated mainly in studies on phytoplankton and macroalgae, but is also found among vascular plants. For example, shade adapted plants maximize their photosynthetic rate at lower light intensities than sun adapted plants. Seagrasses accustomed to higher light regimes have more leaf surface area and less total chlorophyll (Drew 1978, Wiginton & McMillan 1979).

The euphotic zone of phytoplankton is generally taken to be 1% of surface irradiance (Strickland 1958). Eelgrass typically exhibit a depth limitation at 10-25% of surface irradiance (Dennison 1987). The difference between the light requirements of eelgrass and phytoplankton is likely due to the greater respiratory demands of the macrophytes. Seagrasses have extensive below ground respiratory tissue as

well as large respiratory demands for tissues used for both structure and translocation (Dennison 1987). Phytoplankton with their more simplified structure do not have this extensive respiratory demand, and therefore require less light to survive.

Studies suggest depth limits of submersed macrophytes is controlled by light availability. Studies by Chambers & Kalff (1985) and Chambers & Prepas (1988) show that the maximum depth at which freshwater macrophytes are found is positively correlated with underwater light penetration in lakes. Kelly, et al. (1983), also demonstrated the constant relationship between primary productivity and light in macrophyte dominated freshwater rivers.

Light availability is also the primary factor that affects the structure of seagrass meadows (Dennison & Alberte 1982, Dawes & Tomasko 1988). Seagrasses are typically found in coastal areas where depths increase with distance from the shore. In these areas light intensity gradients are formed by the attenuation of light in the water column and by the plant canopy itself (Mazella & Alberte 1986). For example, *Thalassia testudinum*, a tropical species of seagrass, typically exhibits differences in shoot density, leaf area, and chlorophyll content among shallow and deep areas (Dawes & Tomasko 1988). In Chesapeake Bay, the distribution of the seagrasses *Z. marina* and *Ruppia maritima* is related to light requirements with *R. maritima* found in

shallow, higher light areas and *Z. marina* dominating in low light, deeper areas (Wetzel & Penhale 1983). *Z. marina* also possesses the ability to alter its total chlorophyll, ratio of chlorophyll a/b, and shape of leaves in direct response to light availability (Dennison & Alberte 1982, Goldsboro & Kemp 1988). *Myriophyllum brasiliense*, a freshwater submerged plant, has been found to demonstrate a major difference in light dependency between aerial and submersed leaves, such that saturation levels were much lower in the shade adapted submersed leaves than in the sun adapted aerial leaves (Libes 1986). Reports of declines in seagrasses due to increases in water turbidity also provide evidence that light is the major factor determining the distribution of seagrasses (Orth & Moore 1983). While it is true that most seagrasses have adapted to low light habitats of coastal environments, light availability is often the primary limiting factor for seagrass growth (Dennison & Alberte 1985, Dennison 1987).

Wetland sediments, where anaerobic metabolism and sulfate reduction dominate, have been the focus in studies on the effect of accumulation of H_2S on plant responses. Seagrasses are also found in organic rich, highly reducing sediments. Shoot lacunal development and rates of photosynthesis are critical to the downward transport of O_2 from the leaves to the roots of seagrasses (Pulich 1989). When photosynthetic activity is low, roots must tolerate significant periods of anoxia and/or hypoxia (Smith et al.

1984, Smith et al. 1988, Zimmerman et al. 1989).

When the O₂ supply in the sediments becomes limiting, aerobic respiration is replaced by anaerobic metabolic processes (Koch et al. 1990). During these periods of anoxia, heterotrophic anaerobic bacteria use inorganic ions as terminal electron acceptors to break down organic matter (Hines et al. 1989). Where adequate supplies of sulfate and organic matter are present, sulfide is produced in these anaerobic sediments by sulfate reducing bacteria of the genus *Desulfovibrio* (Ingold & Havill 1984). These organisms use sulfate as their terminal electron acceptor for oxidative phosphorylation, the amount of hydrogen sulfide (H₂S) present in marine sediments being dependent on this process (Ingold & Havill 1984, Howarth & Giblin 1983).

In salt marsh sediments, where *Spartina alterniflora* is found, H₂S has been found to be the primary factor inhibiting plant growth and increasing mortality. The mechanisms for this apparent inhibition are not understood (Delaune et al. 1984, King et al. 1982). Several possibilities exist. For example, there is a reduction in ATP generation due to the switch from aerobic to anaerobic metabolic processes (Koch & Mendelssohn 1989). In addition, sulfide accumulation has been found to decrease the activity of root metallo-enzymes, such as important oxidases, used in the electron transport system of respiration (Koch et al. 1990). H₂S may also affect alternate anoxic pathways by limiting the production

of ADH (alcohol dehydrogenase), which is the enzyme catalyzing the terminal step in alcoholic fermentation (Koch et al. 1990). Ethanol, the end product of alcoholic fermentation, when released to the sediment may be a major carbon drain from the plant (Hines et al. 1989). In order to eliminate this carbon drain, fermentative metabolism is maintained only at low levels (Smith et al. 1988). The reduction in nitrogen uptake caused by increases levels of sulfide in sediments surrounding *S. alterniflora* may also be detrimental to its growth and production.

Rice, which is also found in highly reduced, water saturated soils, has been found to be limited in growth, root hair development, and nutrient uptake by increased levels of sediment sulfide (Joshi & Hollis 1977). Chlorosis and stunted growth are indications that rice plants are being stressed by highly reduced soil conditions (Koch & Menselsohn 1989).

The growth of *Salicornia europea*, which is also associated with sulfide containing wetland sediments, has been found to be unaffected by increases in sediment sulfide (Wilkin-Michalska 1985). Sulfide pretreatment inhibited activity of two metallo-enzymes in plants from the upper marsh, such as *Spartina foliosa* and *Scirpus robustus*, but had no effect on enzymes from *S. europea* (Cooper 1984). *Aster tripolum*, a wide ranging halophyte, also appeared to be tolerant of sulfide at concentrations frequently encountered

in salt marshes (Cooper 1984).

The studies cited here have examined the effect of sulfide on growth and biomass of several wetland species. However, no studies have addressed the interactive effect of increases in sediment H_2S and decreases in available light on wetland plants. With reduction in light, seagrasses experience reductions in the rate of photosynthesis. Decreased rates of photosynthesis lead to decreases in O_2 production and therefore the availability of O_2 to aerate the sediment is also reduced. With low levels of O_2 in the sediments, the accumulation of H_2S is enhanced. This increase in sediment sulfide may lead to a reduction in the photosynthetic rate of the plant.

The objectives of this study were to determine the interactive effects of increased levels of sediment sulfide coupled with the reduction of light on the rates of photosynthesis and respiration and response of total chlorophyll and chlorophyll a/b ratios in *Z. marina* in Chincoteague Bay, a shallow coastal lagoon. These objectives were examined both in a field experiment and in controlled microcosm experiment.

METHODS

Chincoteague Bay, a shallow coastal lagoon located along Maryland and Virginia's eastern shore was chosen as the study site for this research (Figure 1). Chincoteague Bay is protected from the Atlantic Ocean by Assateague Island on its eastern side. Inlets are found at the north and south end of the bay with an exchange rate of 7% bay volume/day (Orth et al. 1987). The mean water depth is only 1.1m and the tidal range is approximately 0.3m (Orth et al. 1990). *Z. marina* is found along the eastern portion of Chincoteague Bay.

An eelgrass bed in Chincoteague Bay approximately one mile due east from Greenbackville, VA was chosen as the field site for this research in June of 1991. Cores of *Z. marina* were removed from an area of dense, homogeneous cover and used in the laboratory experiment conducted on the pier at the Greenbackville field station.

The field study consisted of five different sulfide/light treatments (Figure 2). Intact cores were removed temporarily from the site. An agar plate containing a concentration of sulfide was placed in the cored hole. The intact core was then replaced in the hole above the agar plate. The treatments were as follows: control, high light/high sulfide, high light/low sulfide, low light/high

Figure 1: Map of Chincoteague Bay, located along the eastern shores of Maryland and Virginia. The field site for this study is indicated by the black arrow in the eastern portion of the lower bay.

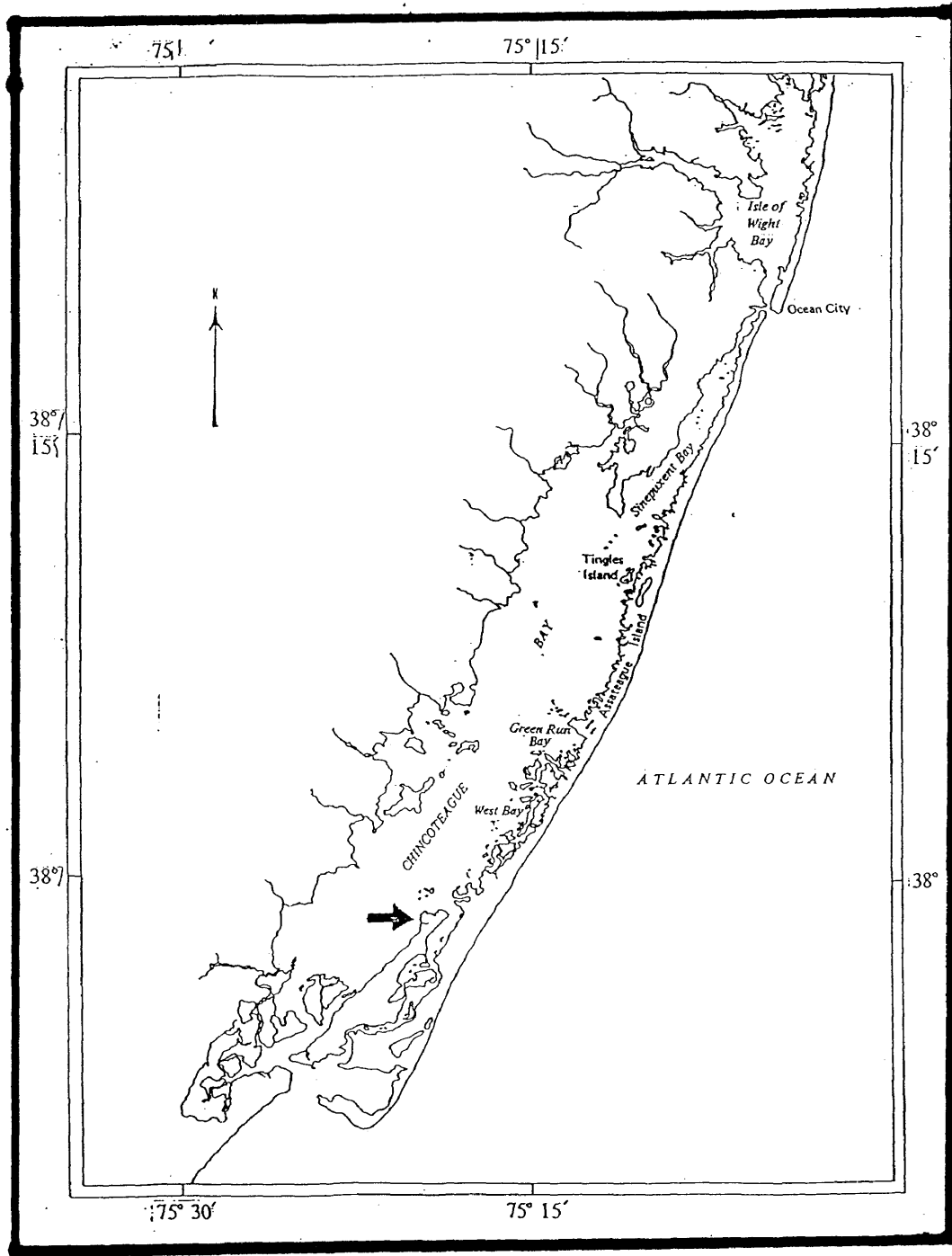
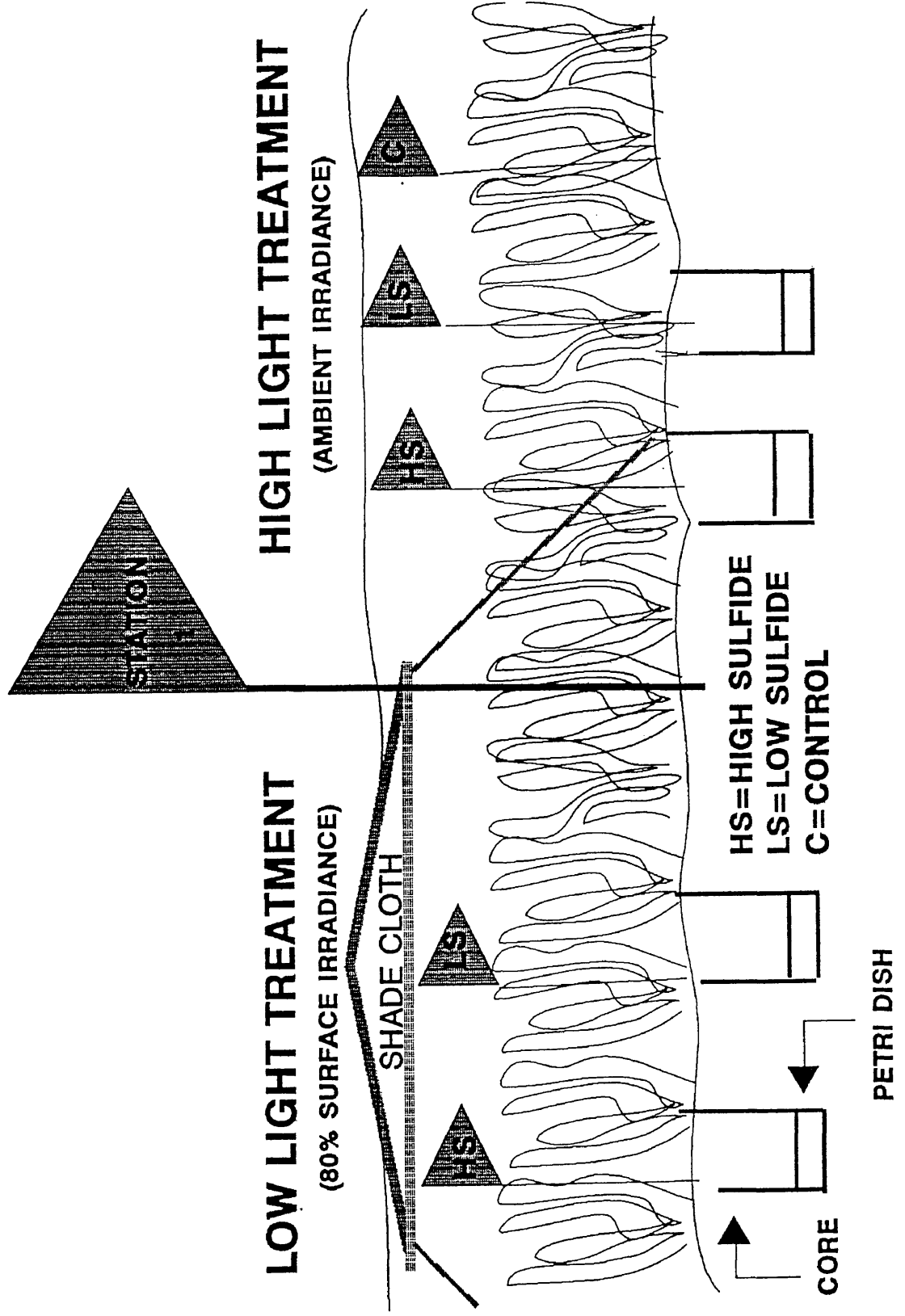


Figure 2: Schematic of the experimental design used in the field experiment. Low light was achieved through the use of shade cloths that reduced surface irradiance by 80%. High light was ambient irradiance. High sulfide (HS) cores had amounts of sodium sulfide added to agar plates to achieve a maximum concentration of 500uM. Low sulfide (LS) cores had no additions to the agar. The control (C) plot was unmanipulated. This station set-up was replicated 5 times.

FIELD EXPERIMENT



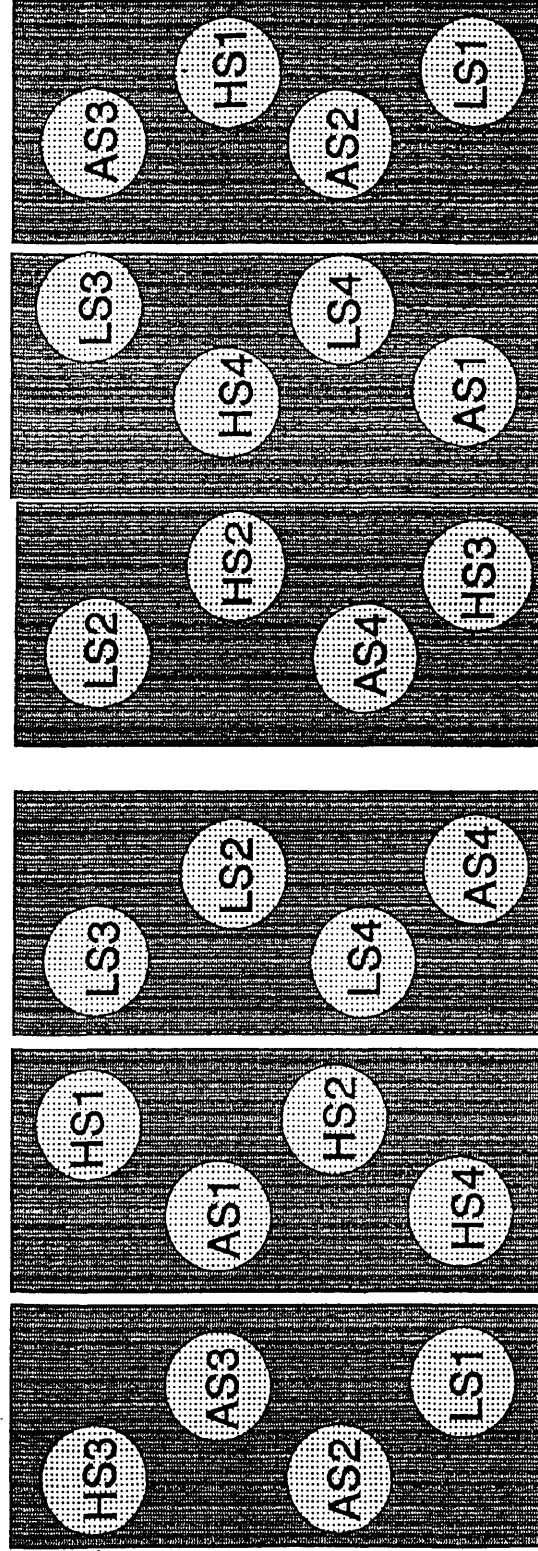
sulfide, and low light/low sulfide. The control was unmanipulated, no coring, no light changes, and no sulfide additions. The high light/low sulfide treatment was considered the manipulative control in that it was subjected to the stress of coring and received ambient light and sulfide. High sulfide treatments had concentrations ($5\text{mM Na}_2 \times 9\text{H}_2\text{O}$) of sodium sulfide dissolved in the agar plates to create a maximum sulfide concentration of $500\mu\text{M}$. Low sulfide treatments represent ambient sediment sulfide and therefore have no additions of sodium sulfide to the agar. Pore water was sampled from the cores using "sippers" which were inserted in the center of the cores. These sippers were made of 1.2 cm diameter PVC pipe, tygon tubing, and $5\mu\text{M}$ mesh. The pore water was analyzed spectrophotometrically to determine actual sulfide concentrations. The design allowed pore water from a depth of 5-15 cm within the core to be extracted. There were five replicates of each of the treatments in the field. Net apparent photosynthesis was measured at the beginning of June 1991 (T_0) and after 21 days.

Twenty four cores were taken from the field site and placed in tanks connected to flowing sea water on the pier at the Greenbackville field station (Figure 3). Cores remained separate and intact throughout the experiment. Agar plates and shade cloths were placed below and above the cores respectively in an attempt to create different sulfide/light treatments.

Figure 3: Diagram of the microcosm experimental design. Low and high light was achieved through the use of shade cloths that decreased insolation by 80% and 20% respectively. Ambient sulfide (AS) cores had no additions of sodium sulfide to the agar plates. Low sulfide (LS) cores had iron sulfide added to agar plates. High sulfide (HS) cores had sodium sulfide added to the agar. Each treatment was replicated five times.

MICROCOSM EXPERIMENT (DOCK)

LOW LIGHT TREATMENT (20% OF SURFACE IRRADIANCE) HIGH LIGHT TREATMENT (80% OF SURFACE IRRADIANCE)



AS= AMBIENT SULFIDE

LS= LOW SULFIDE

HS=HIGH SULFIDE

High, low, and ambient sulfide treatments were created in the microcosms. Ambient sulfide cores had no sulfide added to the agar, creating a control. High sulfide cores had amounts of sodium sulfide ($5\text{mM Na}_2 \times 9\text{H}_2\text{O}$) dissolved in the agar, again to create a maximum sulfide concentration of $1800\mu\text{M}$. Low sulfide cores had iron sulfide (4mM FeSO_4) dissolved in the agar. It has been found that the accumulation of H_2S may be prevented in sediments containing reducible Fe because of the precipitation of sulfide as insoluble FeS (Connell & Patrick 1968). The iron sulfide was thus added in an attempt to bind the ambient sulfide present, thus lowering the sulfide level of the sediment (Joshi & Hollis 1977). Cores were placed randomly in the tanks corresponding to light treatments. Actual sulfide concentrations were again determined by sampling pore water through the use of the sippers. Each sulfide treatment was replicated three times at each light level. Net apparent photosynthesis was measured in the beginning of June 1991 (T_0) and once a week for three weeks on the treated leaves.

Two different light environments were created both in the field and the microcosm experiments. Both high light treatments represented ambient irradiance at the top of the plant canopy. The high light treatment in the field was left unmanipulated. A shade cloth on the pier decreased irradiance to about 55% of surface insolation. The low light environments, both in the field and microcosm, corresponded

to about 20% of surface irradiance in the field. This light compensation point of 20% of surface irradiance is typically the minimum amount of light eelgrass needs to survive. One shade cloth was used to achieve 20% of surface irradiance in the field, while a double cloth was placed over the cores in the microcosm experiment. The actual light intensities under the shades were measured weekly using a 4-PI light sensor. Light sensors with dataloggers that instantaneously measured light and recorded $\mu\text{Em}^{-2}\text{s}^{-1}$ every fifteen minutes, were placed both in the field and on the dock for the month of June 1991 in Chincoteague Bay (Moore unpublished).

In the field and microcosm experiments, net apparent photosynthesis was measured by O_2 evolution using a Clark-type O_2 electrode, Rank Brothers, Ltd. (Dennison & Alberte 1982, Delieu & Walker 1983, Marsh et al. 1986). This type of electrode apparatus is a polarographic cell driven by an externally generated potential difference over a cathode and an anode (Hootsman & Vermaat 1991) and contains a stirring mechanism for constant stirring of the medium.

The growth rate of the eelgrass was determined prior to the beginning of the experiments. Two 2 cm leaf segments from each sample were placed in the electrode chamber. Each 2cm leaf piece was taken from a segment on the second leaf, growth that occurred during the 21 days of the experiments. The electrode chamber contained continuously stirred, O_2 depleted, filtered sea water. The water temperature in the

chamber was kept at a constant temperature using a water bath system as the photosynthetic rate of seagrasses is affected by changes in water temperature (Marsh et al. 1986, Bulthuis 1983, Kerr & Strother 1985, Penhale 1977). The ambient water temperature in June of 1991 averaged 25°C.

The relationship between light and photosynthesis was determined using neutral density filters and light from a 300W tungsten filter bulb. Light intensities ranged from 0-975 $\mu\text{Em}^{-2}\text{s}^{-1}$ and was measured using a 4-PI light sensor. The O_2 electrode was attached to a strip chart recorder which recorded the output in mV cm^{-1} . This reading was converted to $\mu\text{mol O}_2 \text{ min}^{-1} \text{ sample}^{-1}$.

Slopes (y/x) of the converted strip chart measurements were plotted against the irradiance values to obtain a photosynthesis-irradiance (PI) curve for each sample. Dark respiration values were determined from the O_2 output at zero irradiance. The P-max was obtained by averaging the O_2 evolution from the three highest light intensities. A least squares regression was used to estimate I_c , I_k , and the initial slope.

Following the measurement of apparent photosynthesis, the leaf segments were measured on a Licor model 3100 area meter to determine the actual area (dm^2) of the leaf segments. Chlorophyll content of the leaf segments were determined spectrophotometrically (Dennison 1990). The chlorophyll values and leaf area measurements were used to

standardize the photosynthesis and respiration values obtained.

Measurement of the O_2 changes within a medium is a common method used for estimating the photosynthetic rate of submersed vascular plants (Hootsman & Vermaat 1991). However, determining the photosynthetic rate by measuring O_2 evolution may be underestimated due to the possible internal storage of O_2 in lacunar spaces within the plant (Roberts & Moriarty 1987, Zieman 1974).

Seagrasses, as with other aquatic plants, lack stomata and have an interconnection of gas filled spaces called lacunae (Roberts & Caperon 1986, Sorrell & Dromgoole 1986, Smith et al 1988, Smith et al 1984). These spaces are prominent in plant organs which grow where ambient sediment O_2 levels are low (Roberts & McComb 1984). The lacunar cavities provide buoyancy for the plant and can entrap metabolic gases (Sculthorpe 1967). Since Hartman and Brown (1967) published their paper on the accumulation of O_2 and CO_2 in these lacunar spaces, there has been a controversy over the validity of using the O_2 technique to accurately measure productivity in seagrasses (Kemp et al. 1986). It has been suggested that the presence of lacunae could cause an underestimation of photosynthesis measurements, which is based on changes in O_2 concentration within the surrounding medium, as storage, recycling, or translocation of O_2 occurs within these spaces (Kemp et al. 1986, Sorrell & Dromgoole

1986).

Mechanisms for overcoming the problem of O₂ storage in lacunae of seagrasses have been suggested. They include using both small pieces of plant material (Biebl & McRoy 1971), and stimulating the O₂ exchange rate by stirring the surrounding medium (Hootsman & Vermaat 1991, Sorrell & Dromgoole 1986, Sand-Jensen et al 1982). *Z. marina* has a small lacunar volume and under well stirred conditions can reach steady state exchange with the surrounding medium in a matter of minutes (Sand-Jensen et al 1982). Drew (1978) and Wahbeh (1983) concluded errors in photosynthetic measurements using the O₂ technique are small for most seagrasses under stirred conditions. In two different studies, Lipkin et al.(1986) and Kemp et al.(1986) both suggested that the measurement of the net exchange of O₂ is a useful method for field studies due to its simplicity and direct measurement of dark respiration values.

In order to predict the effect of light availability on seagrass productivity and survival, the photosynthetic-irradiance responses of the individual species must be understood. A photosynthesis-irradiance curve is a graphical or mathematical representation of the relationship between rates of measured photosynthesis and light. In general, seagrasses demonstrate a light limited phase of photosynthesis at low light intensities, a linear increase in photosynthesis as light increases, followed by a light

saturation response at highest light intensities (Fourqurean & Zieman 1991). These light response curves are used as predictors of net photosynthesis and growth (Hootsman & Vermaat 1991, Dennison 1987, Dennison & Alberte 1985).

Five parameters can be examined from the relationship between photosynthesis and irradiance. The photosynthetic maximum, P-max, is the rate of net photosynthesis at light saturation. It is the plateau height of the curve (Fourqurean & Zieman 1991). Dark respiration rates are obtained from the point at which the PI curve intersects the y-axis at zero irradiance (Bulthuis 1987). Quantification of respiration in the light, when using the oxygen evolution method is usually assumed to be equal to dark respiration (Hootsman & Vermaat 1991, Fourqurean & Zieman 1991). The rate of photosynthetic increase in response to increases in light, or the initial slope of the curve, is the third parameter. It is in this part of the curve where photosynthetic rate is directly proportional to light (Bulthuis 1987). The light intensity at photosynthetic saturation (I_k) reflects the adaptation of plants to light. Mathematically it is defined as P-max/initial slope (Fourqurean & Zieman 1991). The light compensation point (I_c) is where gross photosynthesis is equal to respiration; i.e., where net photosynthesis is zero.

The differences among all treatments in the field and microcosms, including the unmanipulated control in the field,

were tested using a one-way ANOVA (Analysis of Variance). The interactive effect of light and sulfide manipulations were tested using a two-way ANOVA. Residual plots and Bartlett's test for homogeneity were also used in both analyses.

RESULTS

The average PI curves from the microcosm and field experiments for each treatment level are shown in Figures 4 and 5. Both exhibit typical light limited phases, followed by a linear increase in O_2 evolution as light increases, and leveling off near light saturation.

Photosynthetic parameters were examined on both a per unit chlorophyll and leaf area basis. The results here are presented on a per unit chlorophyll basis. All figures are shown per leaf area in Appendix A. There were no differences in chlorophyll to leaf area ratio among treatments and patterns of treatment response between the two were similar. The P-max and the dark respiration rates of the eelgrass segments were determined from direct measurements. I_c , I_k , and the initial slope of these curves were calculated using a linear regression. In addition to these photosynthetic parameters, total chlorophyll per area and the ratio of chlorophyll a/b were compared among treatments. The means and standard errors of these parameters from the field and microcosm are summarized in Appendix B.

The single and interactive effects of light and sediment sulfide treatments were determined using Analysis of Variance (ANOVA). The p-values are shown in Tables 1 and 2. Lower p-

Figure 4: Graphical comparison of the mean PI curves for the six microcosm treatments and the mean PI curve from time zero.

MEAN PHOTOSYNTHESIS VS. IRRADIANCE CURVES
MICROCOSM EXPERIMENT

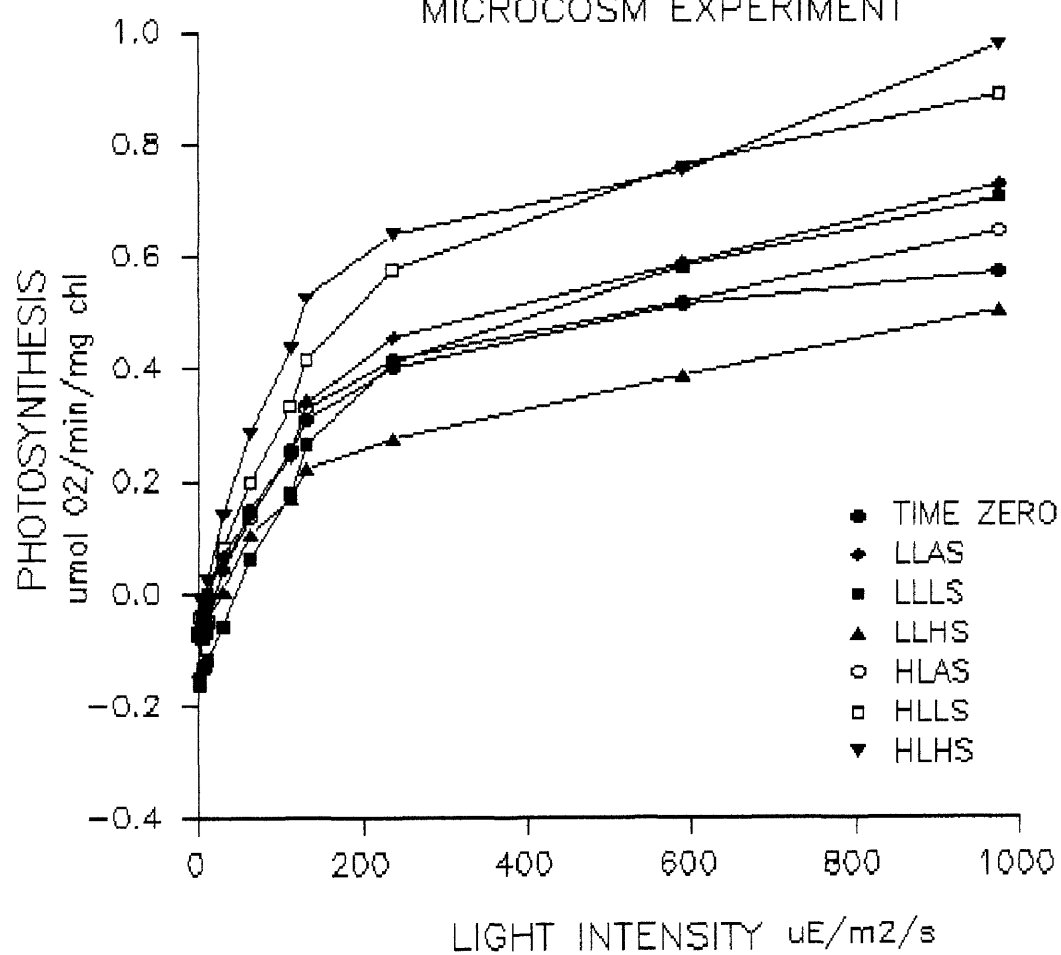


Figure 5: Graphical comparison of the mean PI curves for the five field treatments and the mean PI curve from time zero.

MEAN PHOTOSYNTHESIS VS. IRRADIANCE CURVES
FIELD EXPERIMENT

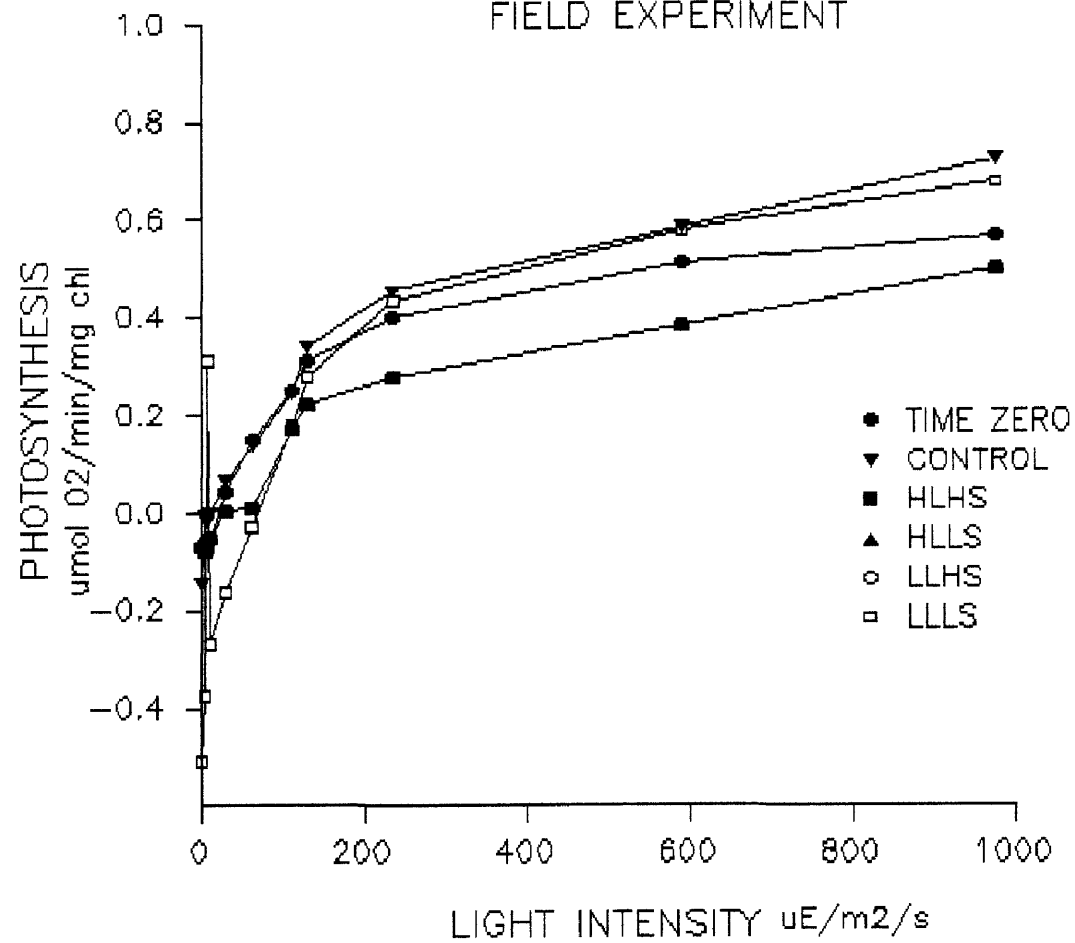


TABLE 1: 1-way and 2-way ANOVA p-values for PI parameters from Field Experiment.

p-Values

P-MAX	Light	0.42
	Sediment	0.50
	Light X Sediment	0.20
	1-Way	0.43
RESPIRATION	Light	0.56
	Sediment	0.52
	Light X Sediment	0.88
	1-Way	0.53
I_c	Light	0.30
	Sediment	0.68
	Light X Sediment	0.45
	1-way	0.10
I_k	Light	0.32
	Sediment	0.37
	Light X Sediment	0.21
	1-Way	0.50
INITIAL SLOPE	Light	0.64
	Sediment	0.30
	Light X Sediment	0.28
	1-Way	0.58
TOTAL CHLOROPHYLL	Light	0.75
	Sediment	0.92
	Light X Sediment	0.69
	1-Way	0.95
CHLOROPHYLL RATIO	Light	0.78
	Sediment	0.25
	Light X Sediment	0.78
	1-Way	0.71

TABLE 2: 1-way and 2-way ANOVA p-values for PI parameters from Microcosm Experiment.

		p-Values
P-MAX	Light	0.79
	Sediment	0.55
	Light X Sediment	0.53
	1-Way	0.56
RESPIRATION	Light	1.00
	Sediment	0.57
	Light X Sediment	0.33
	1-Way	0.82
I_c	Light	0.54
	Sediment	0.72
	Light X Sediment	0.51
	1-way	0.88
I_k	Light	0.49
	Sediment	0.34
	Light X Sediment	0.47
	1-Way	0.34
INITIAL SLOPE	Light	0.72
	Sediment	0.69
	Light X Sediment	0.88
	1-Way	0.53
TOTAL CHLOROPHYLL	Light	0.63
	Sediment	0.76
	Light X Sediment	0.71
	1-Way	0.77
CHLOROPHYLL RATIO	Light	0.51
	Sediment	0.48
	Light X Sediment	0.39
	1-Way	0.68

values suggest statistical significance, or difference between treatments. It is inferred from the high p-values (> 0.05) for all parameters both in the field and microcosms that there is no statistically significant difference among treatment means.

Measured pore water sulfide concentrations for each replicate, both in the field and microcosm experiments, did not consistently reflect application rates in high sulfide and low sulfide treatments. This may explain the lack of difference ($p > 0.05$) observed among treatments. However, irrespective of application rates, a wide range in pore water sulfide (0-500uM in field and 0-1800uM in microcosms) was found among the individual cores.

Due to the lack of light response, it was possible to regroup the replicates from both experiments according to actual sulfide concentrations. The field replicates were combined across light levels and blocked in five groups of increasing 100uM ranges from 0 to 500uM sulfide. The microcosm replicates also were arranged in five groups with the sulfide concentrations ranging from 0 to 1800uM.

Linear regressions were calculated between measured concentrations of pore water sulfide and photosynthetic characteristics of *Z. marina* using these grouped means. The regression lines were tested for significance using a regression analysis. F-values were interpreted and although none of the parameters showed a significance at the 0.05

level, there seems to be a significant response in the P-max ($f=0.07$), respiration ($f=0.11$), and total chlorophyll ($f=0.12$) from the microcosm experiment. All f -values from the field were higher than those from the microcosm. This is probably due to the higher sulfide concentrations achieved in the microcosms.

The P-max and initial slope plots from the field experiment are shown in Figure 6. Vertical and horizontal error bars show the standard errors for both the photosynthetic parameters and the grouped sulfide concentrations. A decrease is illustrated in both parameters with an increase in sulfide concentration. From the microcosm experiment, with a larger sulfide range, the trend suggests a decrease in P-max and respiration (Figure 7), as well as with the initial slope (Figure 8). No distinct difference was illustrated in the I_c or I_k with an increase in sulfide in the field. There is, however, an increasing trend in the I_c and a decreasing trend in the I_k with an increase in sulfide concentration in the microcosm experiment (Figure 9).

The total chlorophyll concentrations suggest an increase per leaf area with increasing sulfide concentration in the field and a decreasing trend in the ratio of chlorophyll a/b (Figure 10). The increasing levels of chlorophyll concentrations with increasing sulfide levels was also observed in the microcosm plants (Figure 11). Total

Figure 6: Mean P-max and initial slopes of the PI curves from the field experiment as a function of the mean grouped sulfide concentrations. Vertical and horizontal error bars show the standard errors for all parameters.

PMAX AND INITIAL SLOPE FIELD EXPERIMENT

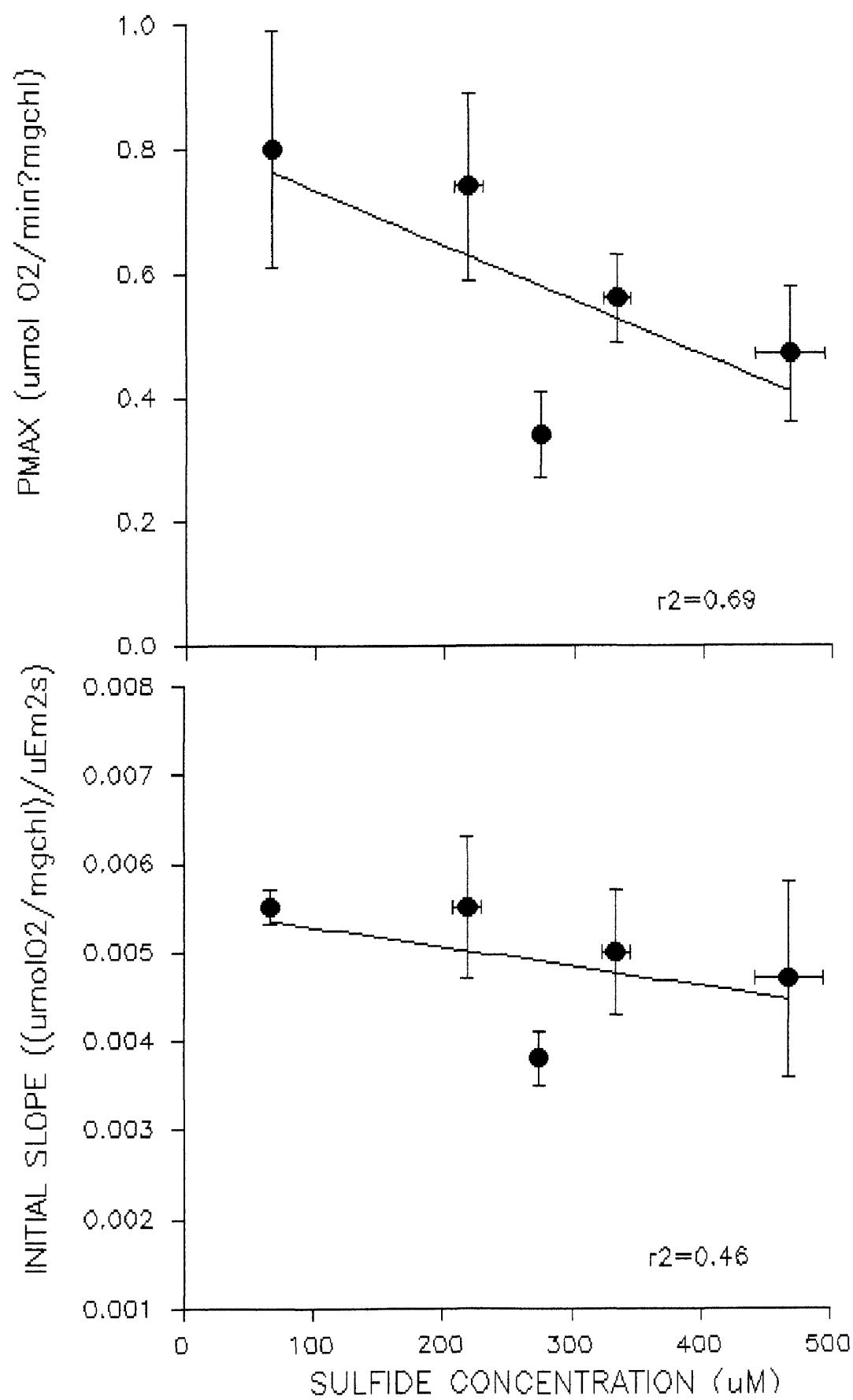


Figure 7: Mean P-max and respiration values, both in $\mu\text{mol O}_2 \text{ min}^{-1} \text{ mgchl}^{-1}$, as a function of mean grouped sulfide concentrations from the microcosm experiment. Vertical and horizontal error bars reflect the standard errors of all the parameters.

PHOTOSYNTHESIS AND RESPIRATION MICROCOSM EXPERIMENT

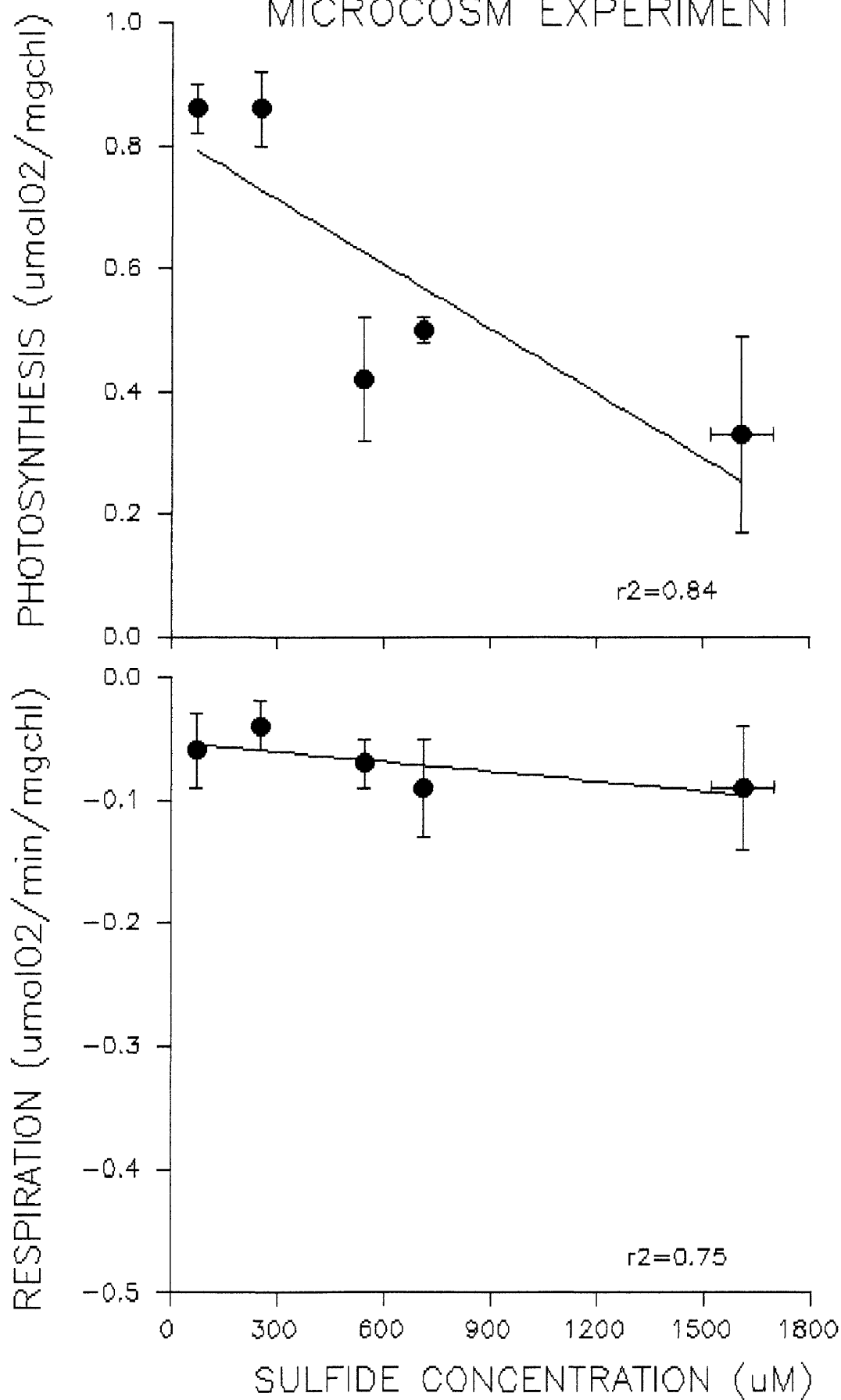


Figure 8: Relationship between the mean initial slopes and increasing sulfide grouped means from the microcosm experiment. Vertical and horizontal error bars show standard errors for both parameters.

INITIAL SLOPE—MICROCOSM EXPERIMENT

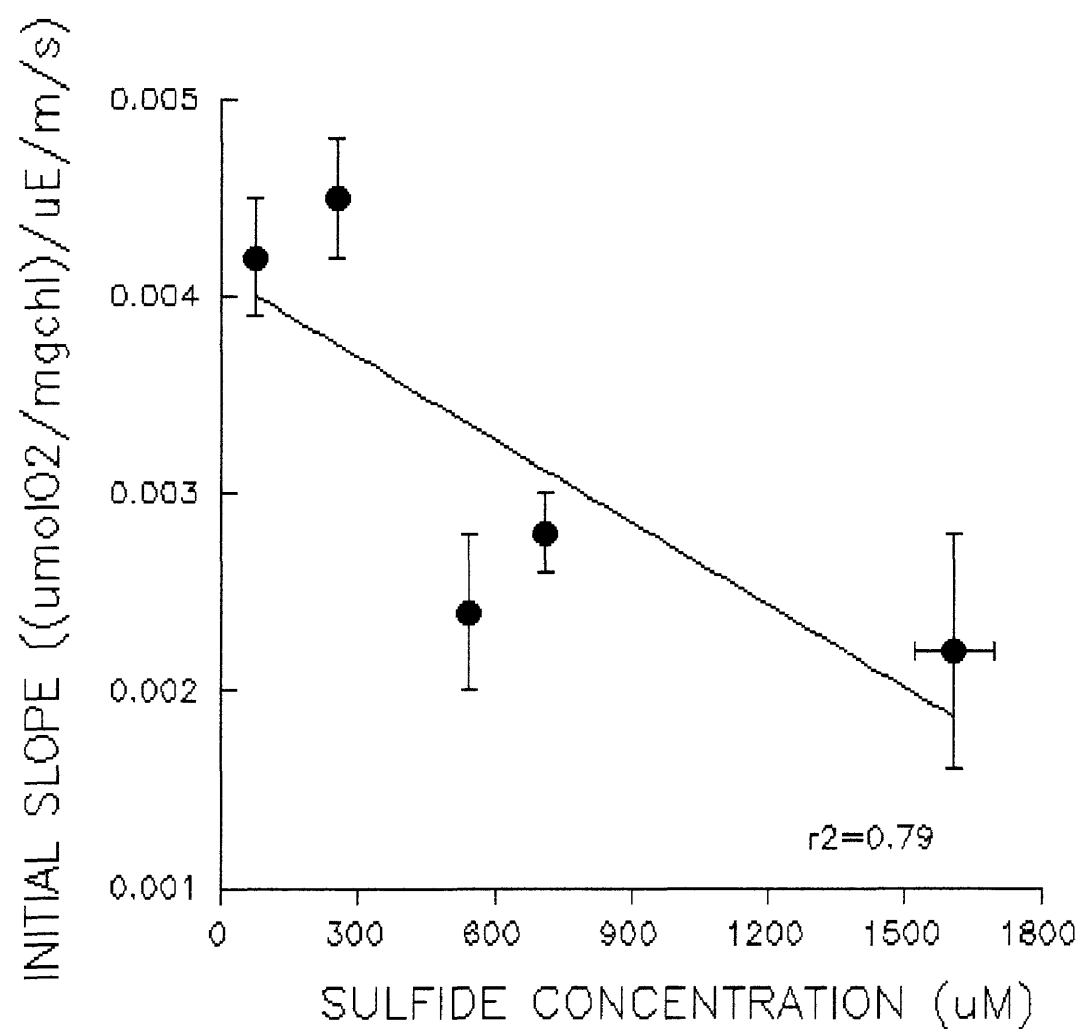


Figure 9: Effect of increasing sulfide grouped means on light compensation (I_c) and light saturation (I_k), both measured in $\mu\text{Em}^{-2}\text{s}^{-1}$, points from the microcosm experiment.

I_c AND I_k —MICROCOSM EXPERIMENT

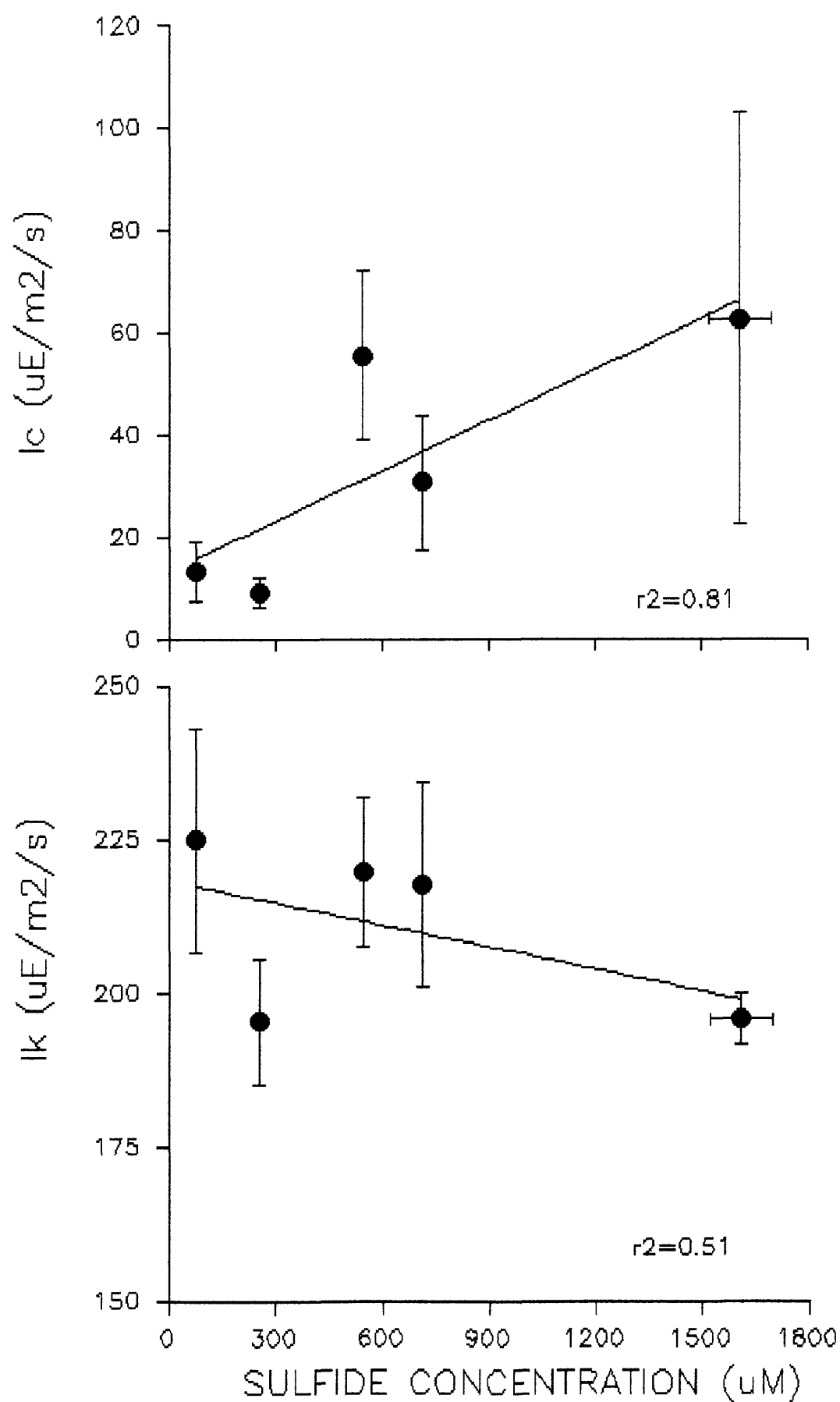


Figure 10: Mean total chlorophyll and ratios of chlorophyll a/b as a function of the grouped mean sulfide concentrations from the field experiment.

CHLOROPHYLL-FIELD EXPERIMENT

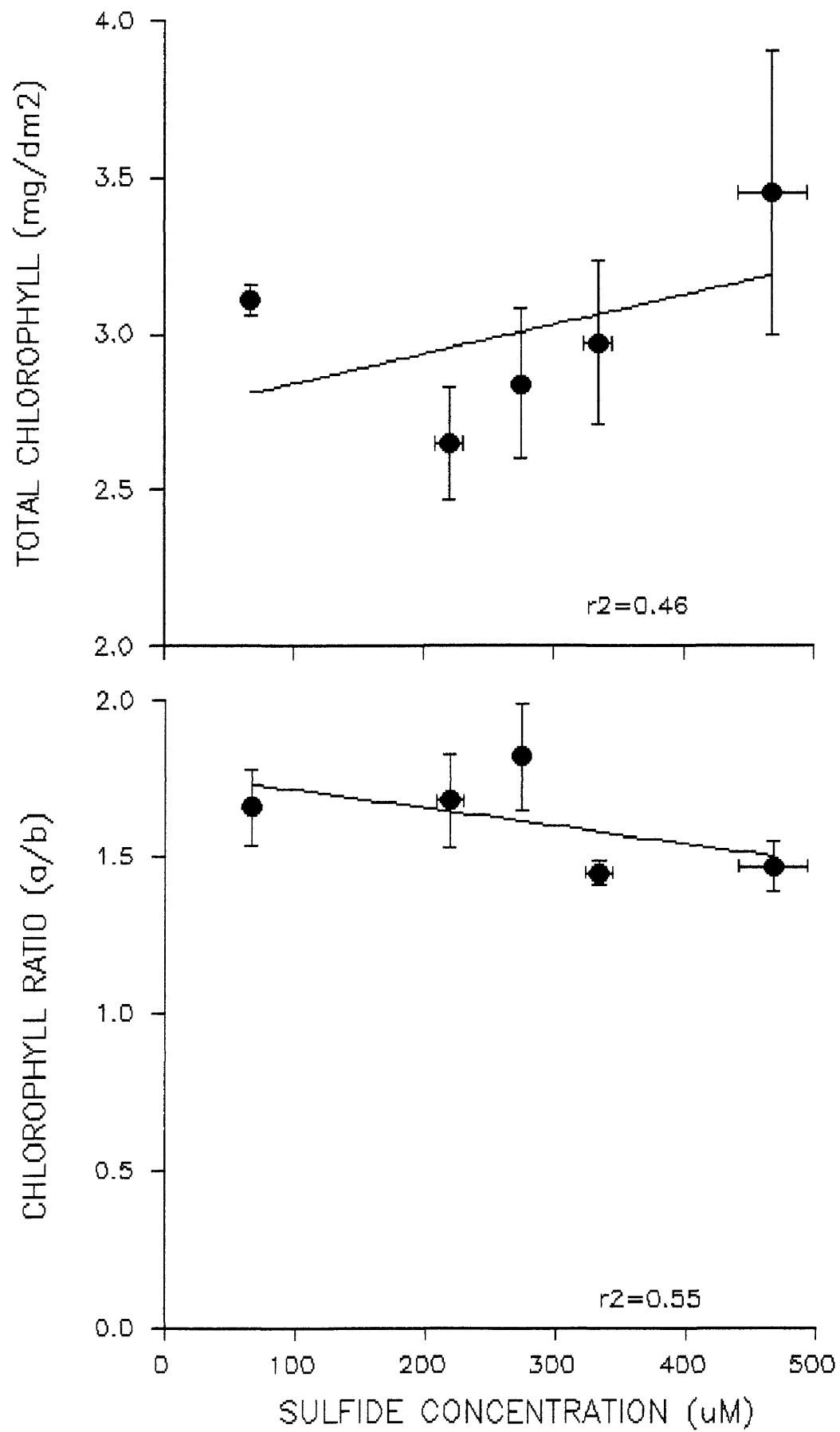
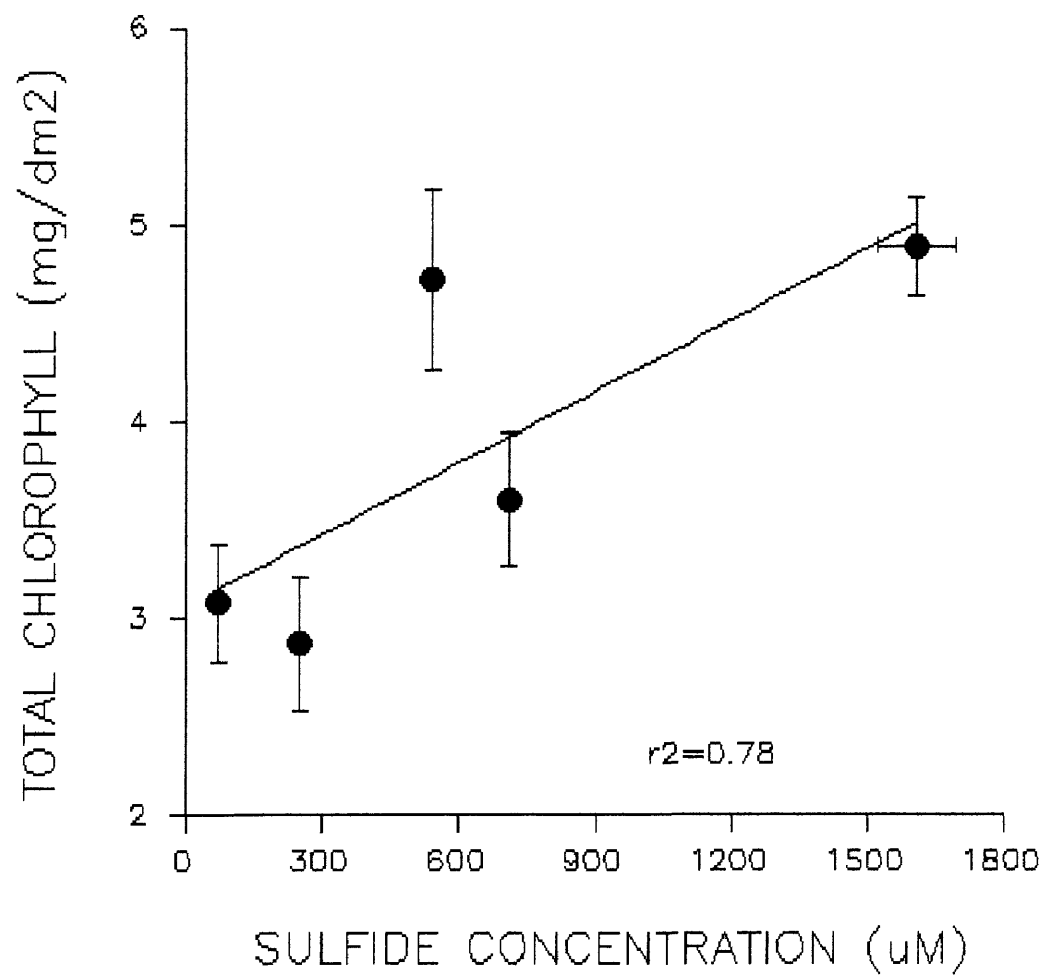


Figure 11: The relationship between mean total chlorophyll concentrations and increasing grouped mean sulfide concentrations from the microcosm experiment.

TOTAL CHLOROPHYLL—MICROCOSM EXPERIMENT



chlorophyll increasing with leaf area in these plants possibly implies a decrease in efficiency of light harvesting with an increase in sulfide concentration. Total chlorophyll levels may be increased in order to optimize light as shade adapted plants do under low light conditions.

The photosynthetic saturation point (H_{sat}) is that portion of the day that light intensities exceed the I_k . Similarly, the photosynthetic compensation point (H_{comp}) is the portion of the day where light intensities exceed the calculated I_c (Dennison & Alberte 1982). These two parameters should be considered when determining if the quantity of light for a particular time period was sufficient to allow normal photosynthetic activity.

From the light records for the month of June and average I_k and I_c values for both the field and microcosm experiments, H_{sat} and H_{comp} could be determined. The actual daily calculated H_{comp} values are shown in Figure 12 for both high and low light treatments for both experiments. Dennison & Alberte (1982,1985,1987) report that H_{comp} values determined using individual leaf segments should average approximately 12 hours per day for the plants to receive sufficient light for normal photosynthetic activity to occur. High light treatments both in the field and microcosm experiments experienced only one or no days of compensating light below 12 hours in June of 1991. The plants grown under low light conditions averaged 10.9-11.3 hours of light above the I_c .

Dennison & Alberte have published several papers comparing these calculated H_{sat} and H_{comp} values under similar low and high light treatments in Great Harbor, Woods Hole, Massachusetts. These values for Woods Hole and those calculated in this study for Chincoteague Bay are shown in Table 3.

Minimal H_{sat} values, with photon flux density sufficient to saturate the leaves, has been determined to be approximately 6 hours (Dennison & Alberte 1985). The mean high light treatment H_{sat} values both in the field and microcosm, greatly exceed this 6 hour minimum. The mean low light treatment H_{sat} values are just below the 6 hour minimum. In fact, these plants were exposed to saturating light for 12 and 10 days in the field and microcosm respectively during the month of study.

The lack of a light response seen in this study is possibly explained by these calculated H_{sat} and H_{comp} values. Even plants grown under low light still experienced adequate hours of compensating and saturating light to maintain normal photosynthetic rates. Although the low light treatments attempted to reduce the available light below the light compensation point for seagrasses, they actually received enough hours of quality light to exhibit no significant difference in photosynthetic parameters as a function of decreased light.

Figure 12: Daily calculated mean H_{comp} values for the high and low light treatments both in the field and microcosm experiments for the month of June 1991 in Chincoteague Bay.

H-Comp JUNE 1991

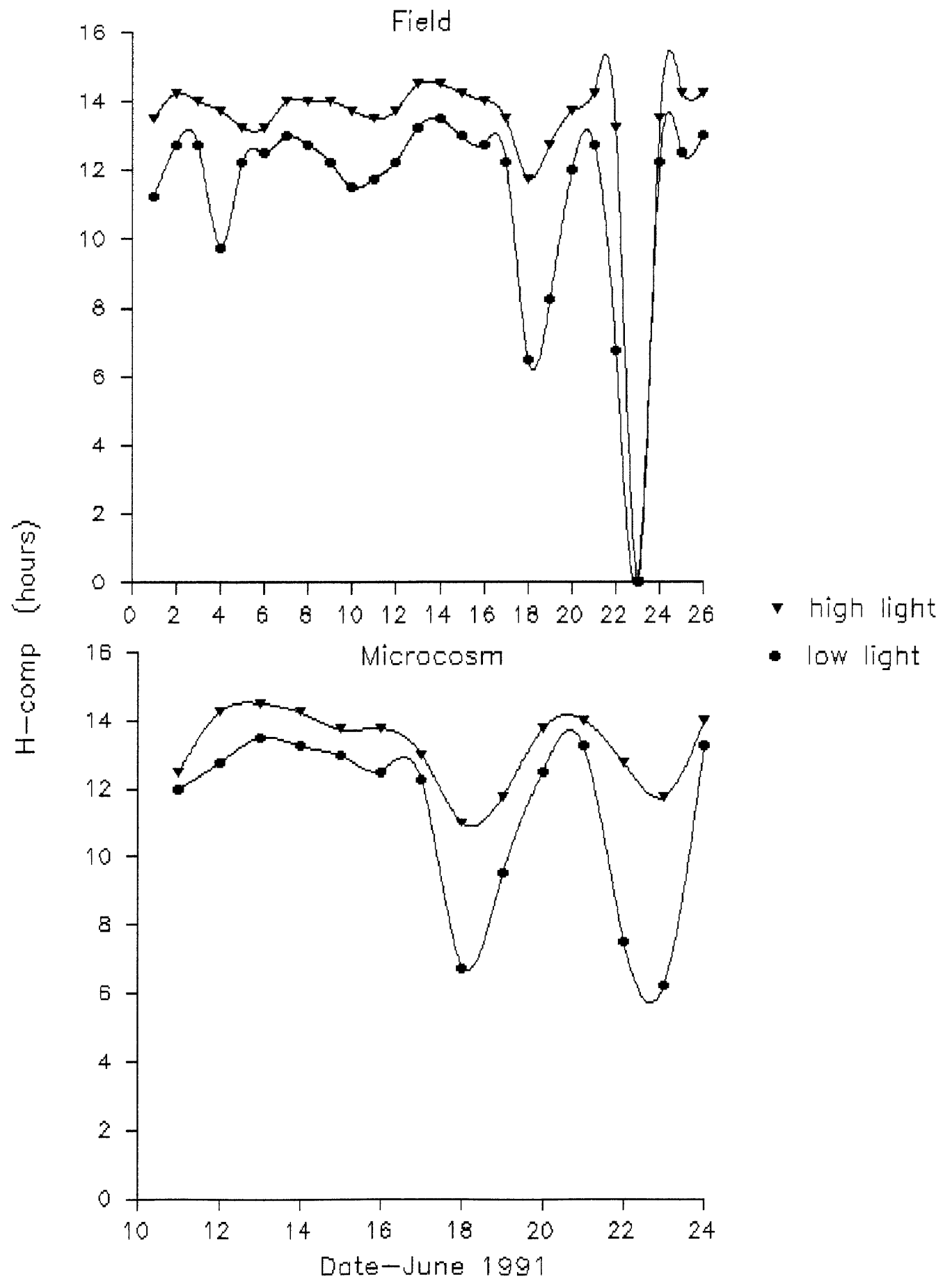


TABLE 3: Comparison of H-comp and H-sat in hours between Chincoteague Bay and Great Harbor, Woods Hole, Massachusetts (Dennison & Alberte).

	H-COMP		H-SAT	
	HIGH	LOW	HIGH	LOW
CHINCOTEAGUE	13.21	11.29	10.73	5.39
WOODS HOLE	12.60	10.90	12.70	5.80

DISCUSSION

Plants adapted to lower light environments display different morphological characteristics compared to their higher light counterparts. For example, aquatic angiosperms that are adapted to lower light typically increase their leaf area and become thinner in order to intercept more light (Goldsborough & Kemp 1988, Spence & Crystal 1970) and freshwater macrophytes of the genus *Potamogeton* increase leaf area up to three fold when grown under low light (Spence & Crystal 1970). Plant adaptations to light may also be observed from changes in pigment concentrations, photosynthetic parameters, and in their response to differences in daily light periods. Examining light adaptations of seagrasses helps to better understand the variability of the environment in which it survives.

In this study, pigment concentrations of plants from high light treatments showed no significant difference in total chlorophyll levels. This is contrary to other studies. For example, marine diatoms, green algae, and freshwater macrophytes all increase chlorophyll content with decreases in light (Kirk 1983, Dring 1986). Eelgrass leaf tissue from Woods Hole , Massachusetts also displays an increase in total chlorophyll under low light conditions (Dennison & Alberte 1985). The lack of difference in pigment concentration

between high and low light plants in this study may be due to the fact that these plants are already adapted to very low light or perhaps the duration of the experiments were too short to allow these angiosperms to adapt.

After 21 days, the eelgrass in Chincoteague Bay displayed no differences in all the photosynthetic parameters in low and high light treatments. Marine algae found growing in lower light level their photosynthetic rate and reach saturation at lower light intensities compared to their higher light counterparts (Kirk 1983). The higher light adapted algae require more light to reach saturation (Kirk 1983). Studies on marine algae, freshwater submersed plants, and *Z. marina* have found differences in the photosynthetic characteristics with reductions in light to levels near saturation (Dennison & Alberte 1985, Dring 1986). These photosynthetic adaptations occur within 24 hours in most algae (Kirk 1983).

A lower respiration rate is often associated with plants that are grown under shaded conditions (Dring 1986). Diatoms and most algae exhibit this characteristic (Kirk 1983). Dark respiration is decreased by about a third in species of *Potamogeton* (Spence & Crystal 1970). With this lower respiratory rate in shade adapted plants, comes a decreased light compensation point (I_c). This is due to the fact that the I_c is where photosynthesis is equal to respiration (Spence & Crystal 1970).

With an increase in pigment concentration in shade adapted seagrasses comes a reduction in the initial slope of the PI curve (Dring 1986). This is partly due to the fact that the more concentrated the pigments become, the less efficiently they collect light, thus lowering the measure of the light gathering efficiency or the initial slope (Kirk 1983).

As was illustrated previously in Figure 12, the daily light periods, H_{comp} and H_{sat} , were different between high and low light treatments. Similar results were also found in a study using eelgrass segments in a more northern coastal habitat (Dennison & Alberte 1985). However, the eelgrass in these other studies displayed differences in photosynthetic characteristics as a function of light, most notably an increase in chlorophyll concentration in shade adapted leaves (Dennison & Alberte 1985). The decrease of H_{sat} and H_{comp} in the low light plants from Chincoteague Bay was enough to cause a difference in growth (Kuhn 1992), but not a difference in the photosynthetic response. The variable daily light regime of Chincoteague Bay may have caused these plants to adapt differently than other plants in similar habitats. It may be that the eelgrass has developed a plasticity and can therefore adapt on a daily basis to changes in light. The low light plants from both experiments experienced several days where their H_{comp} and H_{sat} were well below 12 hours and 6 hours respectively, the time Dennison &

Alberte (1985) have established to be optimal for eelgrass leaf tissue. The several days above the optimal daily light periods were enough to allow these plants to make it through the extremely low light days. It seems these plants have other ways of overcoming or adapting to the highly variable light.

Other studies have addressed the question of the effect of increased levels of sediment sulfide on the growth and production of wetland plants (Koch & Mendelssohn 1989, Joshi & Hollis 1977). However, the effect of the photosynthetic response of plants to increased levels of sediment sulfide has never been addressed.

In both experiments, a decrease in P-max was observed with increasing sulfide levels. The trend is more obvious from the microcosm experiment where the range of sulfide concentrations was higher. One mechanism for this reduction in P-max may be inhibition of enzymes controlling the dark reaction of photosynthesis, such as Rubisco. The P-max of seagrasses and other plants is controlled by the processing time of the dark reaction of photosynthesis (Salisbury & Ross 1985). The Calvin Cycle, as the dark reaction is commonly called, is enzyme controlled. Ribulose biphosphate carboxylase (Rubisco), is the enzyme which catalyzes the combination of CO₂ with ribulose 1,5 biphosphate (RuBP) to form other sugar phosphates and converts some carbon back to RuBP in the Calvin Cycle (Osmond et al. 1980).

The efficiency by which light of low intensities can be utilized in photosynthesis is indicated by the initial slope of the PI curve (Williams & McRoy 1982). With increases in sulfide concentrations in this study, this efficiency is reduced. It seems with a higher stress of sediment sulfide, the eelgrass loses its efficiency to photosynthesize at lower light levels. Higher concentrations of sediment sulfide, greater than 500uM, of the microcosm experiment caused a more drastic decline in the initial slope.

An increase in chlorophyll concentrations was found both in the field and microcosm experiments, with again a more obvious trend from the microcosm. Total chlorophyll increasing with leaf area in these plants implies a decrease in efficiency of light harvesting with an increase in sulfide concentration. The initial slope, which was previously described as the efficiency of utilization of light, also implies this decrease in light capturing efficiency as sulfide levels are increased. Total chlorophyll levels may be increased in order to optimize light gathering as shade adapted plants do under low light conditions (Kirk 1983, Dring 1986).

No trend was observed in the respiratory rate of eelgrass with increasing levels of sulfide from the field experiment. The respiration rate increased with an increase in sulfide in the microcosm experiment (ie. more O₂ was consumed per unit chlorophyll). This implies either the

respiratory demand may be increasing with increased stress of sediment sulfide or that there is an increase in O_2 consumption per unit chlorophyll. In the first, the maintenance cost of the plants may be increased as more O_2 is transported from shoots to roots to replace O_2 that is pumped into the root rhizosphere. Plants exposed to anoxic root environments must have a means for internal O_2 transport to maintain aerobic root respiration (Koch et al. 1990). Alternatively, the second implication would mean there is less chlorophyll in leaves exposed to higher levels of sulfide. Previous comparison of chlorophyll leaf area data revealed that chlorophyll per leaf area increases, not decreases, with an increase in sediment sulfide. Therefore, it is assumed that the maintenance cost (ie. respiratory demand) is increased with an increase in sulfide concentration.

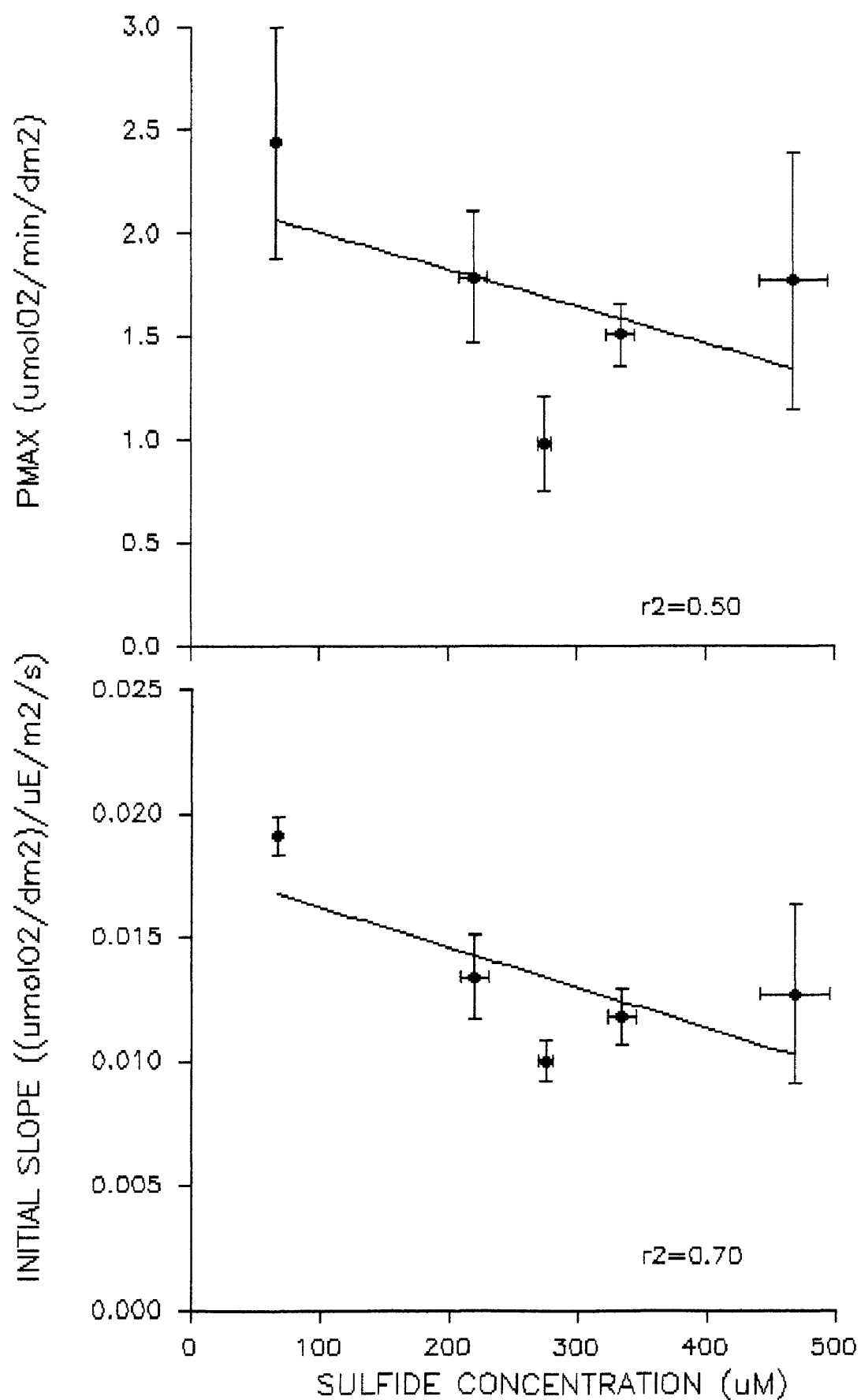
CONCLUSIONS

Despite the lack of significant results, the trends displayed in the photosynthetic response of eelgrass to increases in sediment sulfide are obvious. There was no photosynthetic response of the eelgrass to decreases in light over a 21 day period. This may be due to the ability of the plants in Chincoteague Bay to adapt daily to variable light. It seems there were adequate hours of light, even in the low light treatments, above the H_{comp} and H_{sat} requirements on an average over the study period to allow these plants to photosynthesize at normal levels.

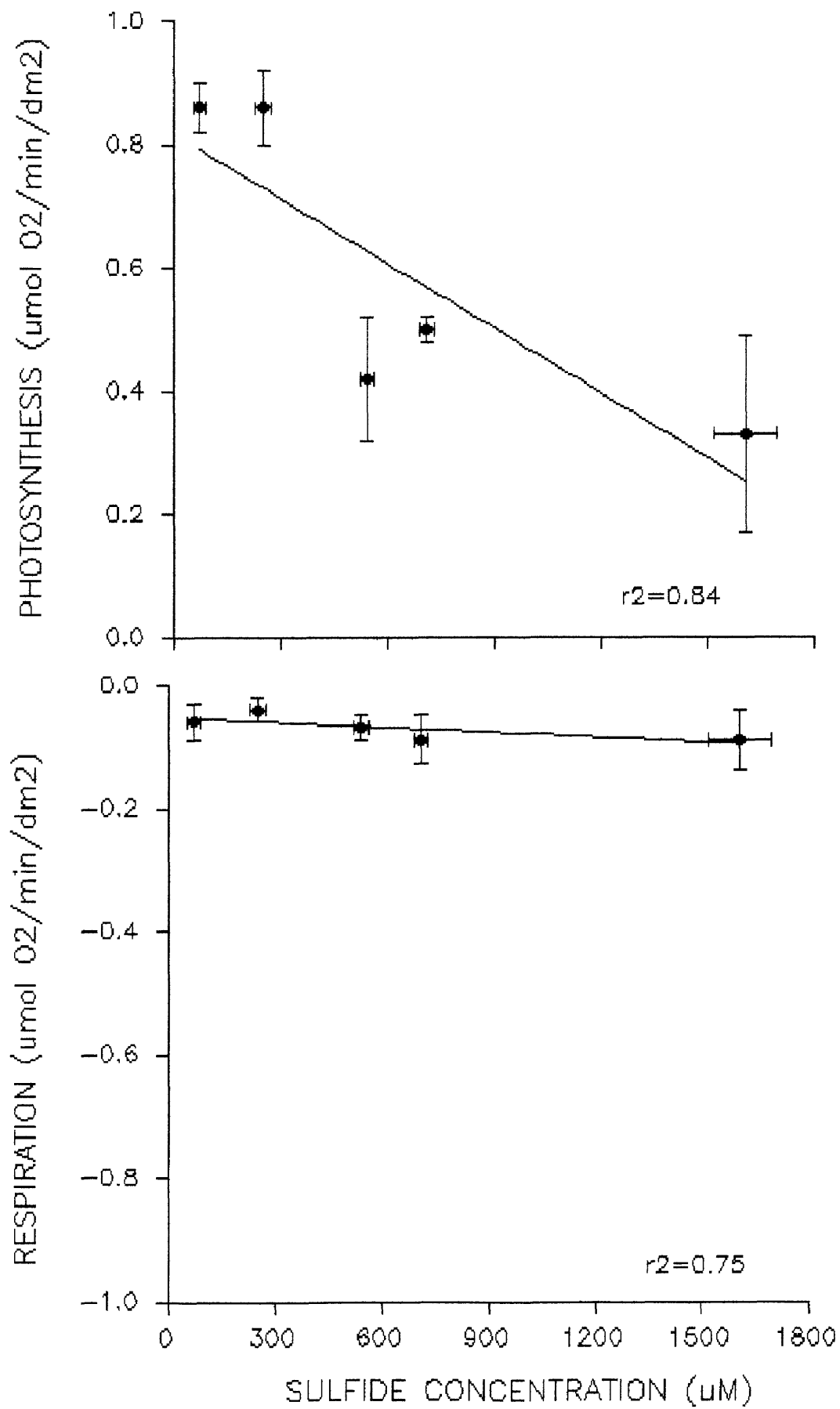
The P-max is reduced in leaves exposed to treatments of sulfide above 500uM. This, again, may be due to the inhibition of enzymes involved in the dark reaction of photosynthesis, which controls the P-max. The respiratory demand of the eelgrass is increased with sediment sulfide levels above 500uM. There is more O_2 consumed per unit chlorophyll. This implies that the maintenance cost of the plants is increased as more O_2 is transported from the shoots to the root rhizosphere. Total chlorophyll is also increased with sulfide concentrations above 500uM. This increase along with a decrease in the initial slope implies a decrease in efficiency of light harvesting as sediment sulfide is increased. Total chlorophyll levels are increased in order to optimize light harvesting.

APPENDIX A: Photosynthetic parameters (P-max, initial slope, respiration, I_c , and I_k) shown on a per leaf area basis for the field and microcosm experiments.

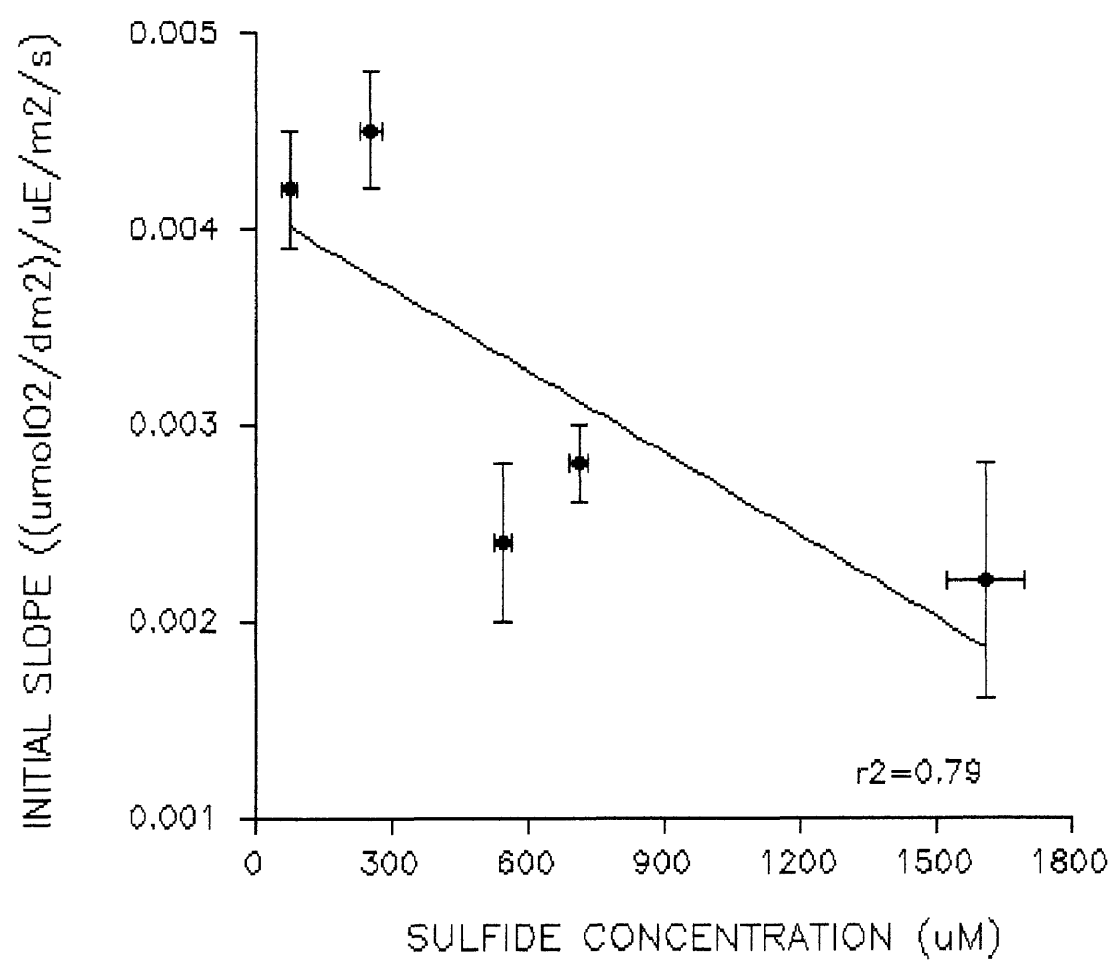
PMAX AND INITIAL SLOPE— FIELD



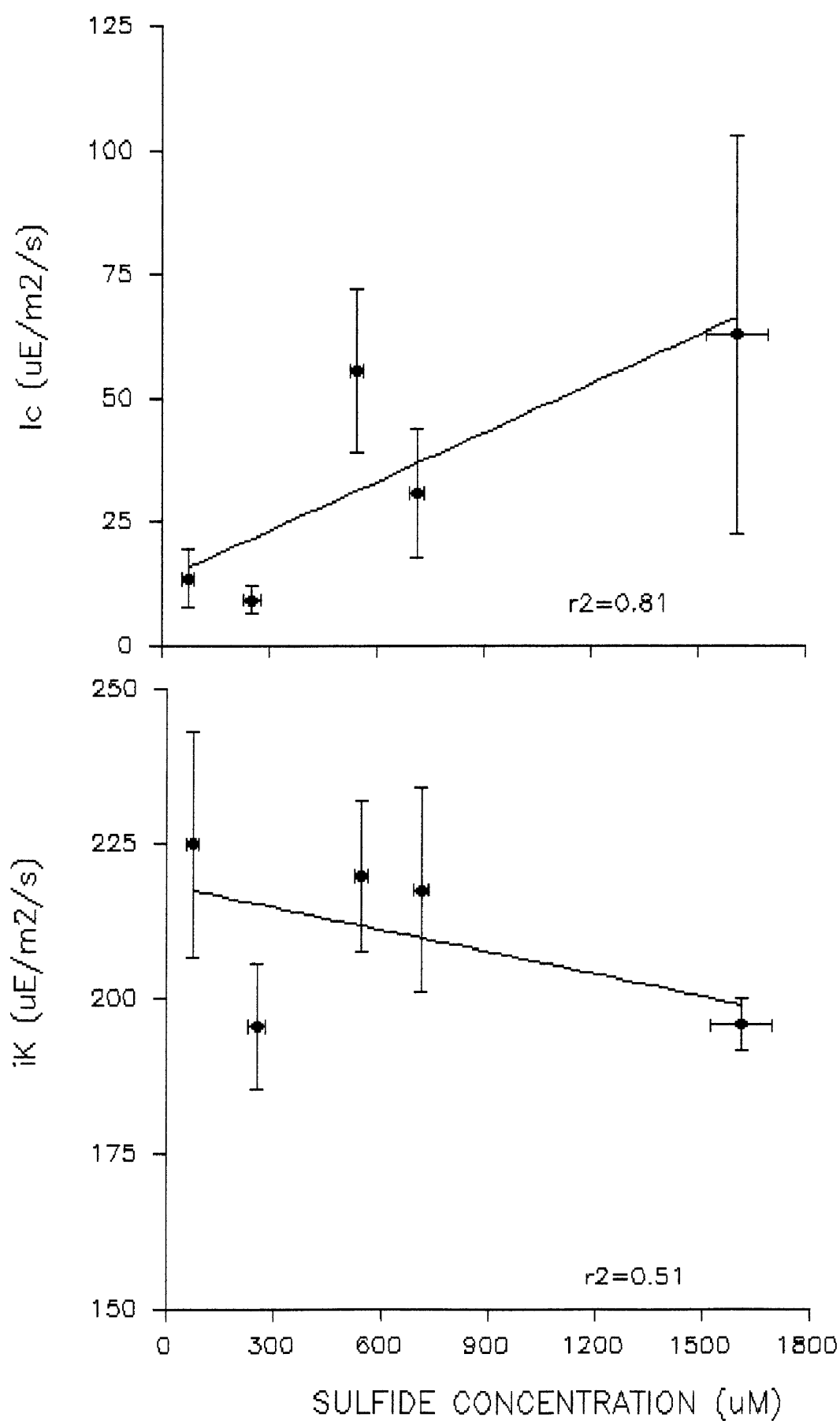
PHOTOSYNTHESIS AND RESPIRATION—MICROCOSM



INITIAL SLOPE—MICROCOSM



Ic and Ik – Microcosm



APPENDIX B

The following tables summarize the means and standard errors of the photosynthetic parameters per unit chlorophyll for the field and microcosm experiments.

TABLE B-1: Maximum net photosynthesis and dark respiration as a function of sulfide and light treatments in eelgrass leaves from microcosm experiment. ($\mu\text{mol O}_2 \text{ min}^{-1} \text{ mg chl}^{-1}$)

	LLAS	LLLS	LLHS	HLAS	HLLS	HLHS
P-MAX	0.59	0.58	0.39	0.53	0.74	0.79
(STD.ERROR)	(0.11)	(0.03)	(0.07)	(0.10)	(0.05)	(0.08)
RESPIRATION	-0.05	-0.10	-0.07	-0.07	-0.04	-0.08
(STD.ERROR)	(0.01)	(0.03)	(0.02)	(0.02)	(0.01)	(0.01)

TABLE B-2: Maximum net photosynthesis and dark respiration as a function of sulfide and light treatments in eelgrass leaves from field experiment. ($\mu\text{mol O}_2 \text{ min}^{-1} \text{ mg chl}^{-1}$)

	CONTROL	HLHS	HLLS	LLHS	LLLS
P-MAX	0.6773	0.3346	0.6402	0.6623	0.5637
(STD.ERROR)	(0.09)	(0.06)	(0.15)	(0.05)	(0.21)
RESPIRATION	-0.1366	-0.2450	-0.3457	-0.3393	-0.4014
(STD.ERROR)	(0.06)	(0.04)	(0.15)	(0.12)	(0.11)

TABLE B-3: Grand means and standard errors of total chlorophyll (a+b) and chlorophyll a/b ratios for eelgrass leaves as a function of light and sulfide treatments from microcosm experiment.

	LLAS	LLLS	LLHS	HLAS	HLLS	HLHS
*TOTAL CHLOROPHYLL	3.51 (0.63)	3.57 (0.11)	4.57 (0.18)	4.26 (0.38)	3.67 (0.25)	3.26 (0.24)
**CHLOROPHYLL RATIO	1.48 (0.02)	1.57 (0.02)	1.54 (0.01)	1.58 (0.06)	1.63 (0.02)	1.70 (0.02)

*mg dm⁻²

**a/b

TABLE B-4: Grand means and standard errors of total chlorophyll (a+b) and chlorophyll a/b ratios for eelgrass leaves as a function of light and sulfide treatments from field experiment.

	CONTROL	HLHS	HLLS	LLHS	LLLS
*TOTAL CHLOROPHYLL	3.103 (0.13)	3.017 (0.07)	2.855 (0.21)	2.773 (0.41)	2.867 (0.42)
**CHLOROPHYLL RATIO	1.586 (0.06)	1.561 (0.04)	1.709 (0.19)	1.465 (0.04)	1.714 (0.22)

*mg dm⁻²

**a/b

TABLE B-5: Compensation Irradiance (I_c), Light Saturation Photon Flux Density (I_k), and Initial Slope as a function of sulfide and light treatments in eelgrass leaves from microcosm experiment.

	LLAS	LLLS	LLHS	HLAS	HLLS	HLHS
I_c^*	38.01	45.93	46.25	39.13	14.93	16.77
(STD.ERROR)	14.6	7.3	17.3	13.8	4.3	3.9
I_k^*	225.27	229.93	201.63	195.93	230.77	188.67
(STD.ERROR)	13.7	5.98	3.23	5.88	9.15	13.7
INT.SLOPE**	0.0029	0.0031	0.0023	0.0031	0.0035	0.0042
(STD.ERROR)	0.0005	0.0001	0.0002	0.0004	0.0003	0.0004

* $\mu\text{Em}^{-2}\text{s}^{-1}$

** $(\mu\text{molO}_2\text{mg}^{-1}\text{chl}^{-1})/\mu\text{Em}^{-2}\text{s}$

TABLE B-6: Compensation Irradiance (I_c), Light Saturation Photon Flux Density (I_k), and Initial Slope as a function of sulfide and light treatments in eelgrass leaves from field experiment.

	CONTROL	HLHS	HLLS	LLHS	LLLS
I_c^*	28.249	89.254	62.307	95.64	103.95
(STD.ERROR)	(1.73)	(1.49)	(7.19)	(2.4)	(2.5)
I_k^*	200.26	218.89	111.12	231.17	92.85
(STD.ERROR)	(43.85)	(33.07)	(14.35)	(35.97)	(17.85)
INT.SLOPE**	0.0050	0.0036	0.0057	0.0051	0.0051
(STD.ERROR)	(.0002)	(0.0003)	(0.0002)	(0.0001)	(.0004)

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